

Effect of habitat on blackcap, *Sylvia atricapilla* nest predation in the absence of corvid predators

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Abstract. Variation in nest survival rates is often ascribed to differences in predator communities. Because corvids are the dominant nest predators in many landscapes with fragmented woodland, their absence may have effect on both the overall nest success and its relationship to habitat features. Nest success of *Sylvia atricapilla* was examined in two habitats in agricultural landscape of SW Slovakia, where corvids were rare/absent. The daily nest survival rate (126 nests) was 0.977 (95% CI: 0.966–0.984) and 0.966 (0.948–0.977) for the egg and nestling stage, respectively, yielding a nest success of 0.52 (0.37–0.64) over a 24-day period. These values are higher than in comparable studies from central Europe, although predation was still the leading cause of nesting failure (more or equal to 71% of 48 failed nests). Correlational evidence suggests link between local absence of corvids and the relatively high nest survival, which was only weakly affected by nest site and habitat characteristics. Nest survival was not detectably higher in forest fragment than in windbreaks and did not increase with distance from forest-field edge or with vegetation concealment. We conclude that both the habitat features and composition of local predator community should be considered when explaining patterns in nest survival rate.

Key words: nest success, nest concealment, agricultural landscape, SW Slovakia

Introduction

There is now good evidence for nest predation being the leading cause of nesting losses in most open nesting songbirds. Yet, there is also a striking lack of consistent patterns in nest predation rates, both within and between species. This has been attributed to variation in predator communities, or to interactive effects of nest site, habitat and behaviour of predators and parents (Dion et al. 2000, Weidinger 2002, Remeš 2005a). The dominant nest predators in many human-altered landscapes are corvids (Andren 1992, Manzer & Hannon 2005) importance of which was suggested to increase with fragmentation of remnant forest habitats and to be higher along forest-field edges (Andren 1992, Ibarzabal & Desrochers 2004). As corvids are visually oriented predators, it is often assumed that nest survival rates should increase with better nest concealment (Martin 1992, Caro 2005).

Here we report on nest success of blackcap, *Sylvia atricapilla* in agricultural landscape of SW Slovakia. The local woodland habitat available for shrub nesting songbirds is represented by two habitat types of different spatial arrangement – fragments of former floodplain

forest and artificial windbreaks. Our previous studies (N é m e t h o v á et al. 1998, N é m e t h o v á 2002) revealed high breeding densities of open nesting songbirds in both these habitats and low density or even absence (no breeding pair in windbreaks since 1997, no field record during this study) of corvids in the area. Studies in other areas of central Europe showed that blackcap nests suffer from intensive predation by diverse predators including corvids (S c h a e f e r 2004, W e i d i n g e r, unpubl. data), that nest success may differ substantially even between adjacent forests of different composition (R e m e š 2003a), while there may be little differences between nesting success in woodlots and narrow riparian strips (W e i d i n g e r 2000). An absence/scarcity of corvids from our study area permitted us to examine, on a correlational basis, an effect of untypical predator community on an overall nest success and on the relationship between nest survival rates and habitat. We hypothesized that nest survival will be equal or higher than in similar habitats elsewhere and not related to those habitat features, that may influence risk of corvid predation.

Study Area

The study was conducted in agricultural landscape of the Podunajská nížina lowland, SW Slovakia (48°01'N, 17°18'E, altitude 125 m), in two types of habitat – windbreaks (WB) and forest fragment (FF). The landscape is dominated by an intensively cultivated arable land; remnants of woodland and windbreaks represent less than 5% of the total area. The WB habitat was represented by network of 12 windbreaks with the total length 7 km (318–1150 m), mean width 16.5 m (6.3–25.6 m) and the total area 12.7 ha. The mean nearest-neighbour distance between windbreaks was 270 m (0–700 m). The dominant tree species are field maple (*Acer campestre*), boxelder (*Acer negundo*), smoothleaf elm (*Ulmus minor*), and poplars (*Populus* spp.). The shrub layer consists of young maples and ashes and black elder (*Sambucus nigra*). The herb layer is restricted to sites with low canopy cover and consists of grasses. The FF represents a remnant of the former floodplain forest. At present it is just a belt of maximum width 400 m and total area 46 ha, disrupted by clearcuts and roads and separated from the nearest windbreak by about 500 m of arable land. The original floristic composition was largely modified. The dominant tree species are poplars; bird-cherry (*Padus racemosa*), ash (*Fraxinus excelsior*) and smoothleaf elm are less frequent. The shrub layer is dominated by the black elder, with admixture of dewberry (*Rubus caesius*), dogwood (*Cornus sanguinea*) and common hop (*Humulus lupulus*). The herb layer is more developed than in WB and consists of nettle (*Urtica dioica*), goldenrod (*Solidago* spp.) and jewelweed (*Impatiens* spp.).

Methods

Field work

Data on breeding densities of the whole bird community, including corvids, were obtained by territory mapping in 1996–2002 (N é m e t h o v á et al. 1998, N é m e t h o v á 2002). During the field work in this study we paid attention to record any possible occurrence of corvids in the area. The breeding density of blackcaps was quantified in 2002 using the territory mapping method, taking into account the position of discovered nests (T o m i a l o j é 1980). The breeding biology was studied in 2001 and 2002. Nests were located by systematically

searching all potential sites in the shrub and herbaceous vegetation from about half of April until the end of June. Nest content was inspected in 1–3 day intervals to determine nesting outcome. Nests from which all eggs or nestlings (age less or equal to 8 days) disappeared were considered depredated. Abandoned nests with intact eggs or dead nestlings were classified as deserted. No nest markers were used and attention was paid to not disturb vegetation around the visited nests. Altogether, nine nest site and vegetation characteristics were measured after the end of the nesting attempt. Cover of the vegetation layer from 20 cm under to 20 cm above the nest was estimated in five categories (0, 25, 50, 75, 100%) within a 0.5 m radius around the nest ($COVER_{NEST}$); cover of the vegetation layers 0–0.3 m ($COVER_0$), 0.3–1 m ($COVER_{0.3}$), 1–3 m ($COVER_1$) and above 3 m ($COVER_3$) was estimated within a 2 m radius around the nest. Height of nest above ground ($HEIGHT_{NEST}$), herb height ($HEIGHT_{HERB}$), shrub height ($HEIGHT_{SHRUB}$) and the distance to the forest-field edge ($DISTANCE$) were measured. Herb and shrub height is a mean of five measurements taken within a 2 m radius of each nest.

Data analysis

The daily survival rate (DSR) of nests was estimated, and the effects of predictors potentially related to nest survival were evaluated by using the logistic-exposure model, which is a generalized linear model with a binomial error distribution and a logistic-exposure link function (Shaffer 2004). This method models nest fate during discrete time periods as a Bernoulli response (0 = failure, 1 = success), incorporating the length of the period in the link function. As the period was considered either the entire nest-visit interval during which nest failed or each survived nest-day (length = 1). Observation intervals of uncertain fate were excluded from analysis by terminating exposure on the last active visit (Manolis et al. 2000). Exposure of successful nests was terminated on the day when nestlings were eight days old (successful nest was defined by survival beyond this age; Weidinger 2007). All analyses were conducted with Proc GENMOD (SAS Institute Inc. 2004).

When evaluating the effects of individual predictors on nest survival, we used an exploratory analysis restricted to a set of models selected a priori to avoid excessive data dredging. The set of candidate models was defined as all possible combinations of relevant habitat predictors with the restriction that each model could contain only one predictor from each of three predictor groups (vegetation cover, heights, spatial characteristics – habitat

Table 1. Pearson correlations among the vegetation characteristics of blackcap nests in forest fragment (n = 72, above diagonal) and windbreaks (n = 54, below diagonal).

| Variable ^a | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|------------------------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1 $HEIGHT_{NEST}$ (m) | x | -0.24 | -0.01 | -0.30 | -0.20 | -0.42 | 0.13 | 0.27 |
| 2 $HEIGHT_{HERB}$ (m) | -0.39 | x | -0.17 | 0.40 | 0.46 | 0.24 | 0.04 | -0.03 |
| 3 $HEIGHT_{SHRUB}$ (m) | -0.05 | 0.21 | x | 0.32 | 0.15 | 0.23 | 0.03 | -0.14 |
| 4 $COVER_{NEST}$ (%) | -0.52 | 0.33 | -0.07 | x | 0.34 | 0.40 | -0.05 | -0.09 |
| 5 $COVER_0$ (%) | -0.49 | 0.05 | -0.04 | 0.43 | x | 0.51 | -0.07 | -0.12 |
| 6 $COVER_{0.3}$ (%) | -0.43 | 0.17 | 0.04 | 0.39 | 0.46 | x | 0.24 | -0.13 |
| 7 $COVER_1$ (%) | -0.03 | -0.07 | 0.20 | 0.02 | -0.08 | 0.04 | x | 0.03 |
| 8 $COVER_3$ (%) | -0.01 | -0.08 | -0.11 | -0.11 | -0.02 | -0.15 | -0.12 | x |

^a Height of the nest above the ground, herb height, shrub height, cover of the vegetation layers at the nest height, 0–0.3 m, 0.3–1 m, 1–3 m and above 3 m.

type or distance to forest-field edge) under the assumption that predictors are somewhat redundant within these groups (Table 1). Models containing all possible combinations of time dependent predictors (year, Julian date, nesting stage) but no habitat predictors were also included. Resulting sets comprised 79 candidate models.

The adequacy of the candidate models was assessed according to the Akaike's information criterion with finite sample correction (AIC_c), following guidelines by Burnham & Anderson (2002). All models that differed in AIC_c from the best supported model (the model with lowest AIC_c) by a factor less than 2 were considered to be similarly supported. Parameter estimates was calculated averaged across the set of candidate models using model weights (w), which reflect both the uncertainty associated with the given model and the uncertainty in selecting that model. For each predictor we present also its cumulative weight (cw) which is a sum of model weights over all models containing that predictor.

Results

Breeding biology

In all, 101 blackcap territories were mapped in 2002; the breeding density was higher in forest fragment (5.5 pairs/ha) than in windbreaks (3.4 pairs/ha). A total of 126 active nests were found which provided data useful for analysis of nest survival. Altogether, 20 plant species supported nests, of which black elder, smoothleaf elm and field maple accounted for 67% of all cases. The measured nest site characteristics were similar in WB and FF, except of the distance to forest-field edge (Table 2). The median laying date was 6 May (WB) and 3 May (FF) in 2001 and 3 May (WB) and 27 April (FF) in 2002. The constant survival model (without covariates) estimated the daily survival rate as 0.973 (95% CI: 0.964–0.980), yielding a nest success estimate of 0.51 (0.42–0.61) over a 24-day period. The stage-specific survival model estimated the daily survival as 0.977 (0.966–0.984) and 0.966 (0.948–0.977) for the egg (laying + incubation) and nestling stage, respectively, yielding a combined nest success estimate of 0.52 (0.37–0.64) over a 24-day period. The overall variation in daily survival rate between the nesting stages, years and habitats was relatively low given the wide

Table 2. Nest site characteristics of the blackcap in the two habitats.

| Variable ^a | Forest fragment (72 nests) | | | Windbreaks (54 nests) | | |
|-----------------------------|----------------------------|------|--------|-----------------------|------|--------|
| | Mean | SD | Median | Mean | SD | Median |
| DISTANCE (m) | 37.2 | 22.3 | 32.5 | 6.1 | 5.0 | 5.0 |
| HEIGHT _{NEST} (m) | 1.2 | 0.6 | 1.2 | 0.8 | 0.4 | 0.7 |
| HEIGHT _{HERB} (m) | 0.5 | 0.3 | 0.5 | 0.6 | 0.3 | 0.6 |
| HEIGHT _{SHRUB} (m) | 1.6 | 0.5 | 1.6 | 1.3 | 0.6 | 1.3 |
| COVER _{NEST} (%) | 80.0 | 16.6 | 83.3 | 78.9 | 19.1 | 83.3 |
| COVER ₀ (%) | 85.8 | 27.6 | 100.0 | 73.7 | 33.2 | 90.0 |
| COVER _{0.3} (%) | 74.2 | 28.0 | 80.0 | 67.4 | 22.1 | 60.0 |
| COVER ₁ (%) | 78.6 | 21.8 | 80.0 | 77.8 | 19.3 | 80.0 |
| COVER ₃ (%) | 60.8 | 33.6 | 60.0 | 83.7 | 22.7 | 100.0 |

^a Distance to the forest-field edge, height of the nest above the ground, herb height, shrub height, cover of the vegetation layers at the nest height, 0–0.3 m, 0.3–1 m, 1–3 m and above 3 m.

Table 3. The daily survival rates (DSR) of blackcap nests estimated by the constant survival (without covariates) logistic exposure model for the two habitats and two nesting stages.

| | 2001 (48 nests) | | | 2002 (78 nests) | | |
|-----------------|-----------------|-------|-------------|-----------------|-------|-------------|
| | n | DSR | 0.95 CI | n | DSR | 0.95 CI |
| Habitat | | | | | | |
| Forest fragment | 284 | 0.980 | 0.959 0.992 | 708 | 0.975 | 0.962 0.985 |
| Windbreak | 337 | 0.964 | 0.942 0.980 | 357 | 0.970 | 0.949 0.984 |
| Stage | | | | | | |
| Egg | 376 | 0.982 | 0.966 0.992 | 701 | 0.973 | 0.960 0.984 |
| Nestling | 245 | 0.954 | 0.924 0.975 | 364 | 0.973 | 0.954 0.987 |

n = effective sample size – the total number of nest-days for the successful (survived) observation intervals plus the number of observation intervals during which nest failed.

confidence intervals of the estimates (Table 3). Nest loses (n = 48 failed nests) were caused mostly by predation (71%) and nest desertion (23%), or remained unknown (6%). The share of predation varied from 69% to 83% among the habitat-year samples. These are minimum estimates as we suspect that also at least 60% of the nest desertions (n = 9 nests) was a consequence of partial predation.

Effect of habitat on nest survival

Addition of habitat predictors improved fit over the constant survival model ($\Delta AIC_c = 3.4$). The best supported of the most parameterized models (K=4) fitted the data reasonably well (Hosmer-Lemeshow goodness-of-fit test: $\chi^2 = 8.8$, df = 8, P = 0.36). Seven of the 79 candidate models received similar support ($\Delta AIC_c < 2$; Table 4). Of these, the best approximating and, at the same time, the most parsimonious model contained only the effect of herb height. However, the weight of this model as well as the cumulative weight of the seven best models was very low (8% and 37%, respectively). Nest survival tended to increase with lower herb height, longer distance to forest-field edge, more vegetation cover in layers above 3 m and 0.3–1 m, and tended to be higher in forest fragment than in windbreaks (Table 5). The herb

Table 4. Model fitting results for the nest survival of blackcap. Models are compared according to number of parameters (K), model deviance (Dev), Akaike’s Information Criterion corrected for sample size (AIC_c), the difference in AIC_c from best-fitting model (ΔAIC_c), and model weight (w). Only 7 best supported models are given.

| Model ^a | K | Dev | AIC_c | ΔAIC_c | w |
|--|---|-------|---------|----------------|------|
| HEIGHT _{HERB} | 2 | 324.5 | 328.5 | 0.0 | 0.08 |
| HEIGHT _{HERB} + COVER ₃ + DISTANCE | 4 | 321.0 | 329.0 | 0.5 | 0.06 |
| HEIGHT _{HERB} + COVER ₃ + HABITAT | 4 | 321.2 | 329.2 | 0.7 | 0.05 |
| HEIGHT _{HERB} + COVER ₃ | 3 | 323.2 | 329.2 | 0.7 | 0.05 |
| HEIGHT _{HERB} + DISTANCE | 3 | 323.3 | 329.3 | 0.8 | 0.05 |
| HEIGHT _{HERB} + COVER _{0.3} | 3 | 323.6 | 329.6 | 1.1 | 0.04 |
| HEIGHT _{HERB} + HABITAT | 3 | 323.8 | 329.8 | 1.3 | 0.04 |
| CONSTANT | 1 | 329.9 | 331.9 | 3.4 | 0.01 |

^a For explanation of habitat variables see Table 2.

Table 5. Parameter estimates and cumulative weights of predictors from the best supported models of blackcap nest survival (Table 3).

| Effect | Single effect models | | Averaged over models | | Cumulative weight |
|---------------------------|----------------------|-------|----------------------|-------|-------------------|
| | estimate | SE | estimate | SE | |
| HEIGHT _{HERB} | -0.937 | 0.399 | -0.557 | 0.335 | 0.608 |
| DISTANCE | 0.011 | 0.007 | 0.004 | 0.004 | 0.346 |
| COVER ₃ | 0.005 | 0.005 | 0.002 | 0.002 | 0.262 |
| HABITAT (FF) ^a | 0.345 | 0.293 | 0.090 | 0.104 | 0.245 |
| COVER _{0,3} | 0.003 | 0.006 | 0.001 | 0.001 | 0.122 |

^a Effect for forest fragment; reference category = windbreak.

height and cover above 3 m were the most informative of the “height” and “cover” predictors, respectively, while the distance to forest-field edge was more predictive than habitat type. Of the models containing only the time-dependent predictors, the model with a single effect of date ($\Delta AIC_c = 2.8$) or nesting stage ($\Delta AIC_c = 3.6$) ranked relatively best. We explored a posteriori the utility of combining habitat and time predictors. Addition of date to habitat predictors did not improve an overall fit of the models (herb height + date: $\Delta AIC_c = 0.1$).

Discussion

Nest success of blackcaps in our study (52%) was, on average, higher than in comparable studies (based on “Mayfield” estimate and intensive nest searching, in fragmented deciduous woodland) from central Europe where the most blackcap populations reached nest success about 30% (Weidinger 2000, 2002, 2007, Remeš 2003a,b, Schaefer 2004). Yet, predation was still the leading cause of nesting failure as elsewhere. Relatively high nest success can not be ascribed to breeding density or nest sites used (supporting plant, height above ground), all of which were well within the range of values reported from the central Europe (Glutz 2001, Weidinger 2000, Remeš 2003b). On the other hand, our results are in concert with the unusual composition of local predator community. It appears that the absence or very low abundance of an important class of nest predators – corvids from our study area was not fully compensated by an increased predation by the other predators. Although compensatory nest predation may be common in game species (e.g. Kauhala 2004), our correlative data are in agreement with the few studies of farmland songbirds showing that removal of potential nest predators led to increased nest survival (Stoate & Szczur 2001, Donald et al. 2002).

We lack exact knowledge about identity of nest predators at our site. Yet, an indirect evidence suggests relatively low importance of corvids – parallel study (conducted on the same localities) showed that birds destroyed only about 5% of 574 artificial nests mimicking real blackcap nests, which equals to 7% of total predation (Lavrínčíková 2003). This is in contrast with similar studies in other areas, where birds accounted for about 50% of total predation on artificial blackcap nests (Weidinger 2002, Remeš 2005b). Videotaping of real blackcap nests in central Europe revealed similarly high rates of corvid predation (65% of 40 depredated nests, Schaefer 2004; 40% of 55 depredated nests, Weidinger, unpubl.). This suggests that beak imprints in plasticine eggs may represent a reliable index of avian predation on this species and that our inferences about low corvid

predation in this study are valid. As the rodent predation on artificial blackcap nests at our study plots was relatively very high (87% of 415 depredated nests, L a v r i n ě í k o v á 2003) we speculate that small rodents could depredate also the real blackcap nests, although the importance of mice as predators of active (as opposed to artificial) shrub nests is largely unknown in the central Europe (5% of 40 depredated nests, S c h a e f e r 2004; none of 177 depredated nests, W e i d i n g e r, unpubl.).

Nest survival was only weakly affected by nest site characteristics. Our results thus do not support the common wisdom that nest survival increases with better nest concealment (M a r t i n 1992, H o i - L e i t n e r et al. 1995, C a r o 2005). One possible reason for absence of an overall effect of nest concealment is that parental behaviour (nest attentiveness, frequency of feeding trips, nest defence) may compensate for an effect of nest site (W e i d i n g e r 2002, R e m e š 2005a). Second, different nest sites may be exposed to different predators, the overall predation rate being unrelated to any particular nest site (R a n g e n et al. 1999, D i o n et al. 2000, W e i d i n g e r 2002, T h o m p s o n & B u r h a n s 2003, R e m e š 2005b). Finally, nest concealment may be unimportant in the absence of visually hunting predators (corvids in this study), when the local predators search for nests by means of olfactory sense or when they encounter nests incidentally as a result of differential space use (W i t h 1994, S c h m i d t et al. 2001, S c h m i d t & O s t f e l d 2003).

Of the nest site characteristics examined in this study, only the height of herb layer detectably influenced nest survival – nests with tall herb vegetation under the nest were more likely to be depredated. This is in line with our suggestion that the predator of blackcap nests could be rodents. Small mammals concentrate their activity into dense herbaceous vegetation to protect themselves from avian predators (F e d r i a n i & M a n z a n e d a 2005), thus increasing probability of encounter with nests placed in/above it (W i t h 1994, R a n g e n et al. 1999, W e i d i n g e r 2002, R e m e š 2005b).

Similar to nest site, also the spatial habitat characteristics only little affected nests survival. Contrary to conventional expectation (e.g. C h a m b e r l a i n et al. 1995, M a j o r et al. 1999), nest survival was not detectably higher in forest fragment than in windbreaks and did not increase with distance from forest-field edge in any habitat. The absence of edge effect can be partly attributed to the linear nature (windbreaks) and small size (forest fragment) of habitat patches in this study. Given that edge effect on nest predation is supposed to extend up to 50 m deep into the forest (P a t o n 1994, B a t a r y & B a l d i 2004) all of our study plots represented edge habitat, regardless of their spatial arrangement. An occurrence and spatial extent of edge effect is contingent upon the landscape context and local predator community. Hence, our results are in line with earlier blackcap studies (W e i d i n g e r 2000) and a generally weak evidence for edge effects in agricultural landscapes of the central Europe (B a t a r y & B a l d i 2004), as well as with the local predator composition. Corvids, whose foraging activity may be associated with forest-field edges (I b a r z a b a l & D e s r o c h e r s 2004), were absent/rare from our area. On the other hand, small rodents, whose activity may be relatively less related to forest edges (H a n n o n & C o t t e r i l l 1998), especially where dense vegetation cover is not restricted to edges (K o l l m a n n & B u s c h o r 2002), were the suspected predators. We should note, however, that our data from forest fragment were not replicated on the habitat scale, simply because of the scarcity of this habitat in the local landscape.

Taken together, correlational evidence suggests link between local scarcity of corvid predators and blackcap nest survival, which was relatively high and not related to nest

concealment and spatial habitat characteristics (distance to edge). Nest losses were presumably due to incidental predation by rodents, which was associated with an occurrence of tall ground vegetation under the nest, but not with the other nest/habitat variables. We conclude that both the habitat features and composition of local predator community should be considered when explaining variation in nest survival patterns.

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